## CORRESPONDENCE

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## NATURAL SELECTION AND FITNESS

To the Editor, The Eugenics Review

Sir,—It is disturbing to have a scientist accuse his colleagues who disagree with him on scientific issues of a "lack of understanding." This accusation has been levelled, directly or by implication, by Sir Julian Huxley against Professor P. B. Medawar and myself.\* One of the things which we lack understanding of is natural selection. We are guilty of "geneticism," because we describe what has been variously referred to as Darwinian fitness, selective value, or adaptive value of a genotype as the contribution which its carriers make to the gene pool of the succeeding generation relative to the contribution of other genotypes. Natural selection tends to maintain or to enhance the Darwinian fitness. To Sir Julian this is "nonsensical," because natural selection "produces biological improvement, resulting in a higher total and especially a higher upper level of evolutionary fitness, involving greater functional efficiency, higher degrees of organization, more effective adaptation, better self-regulating capacity, and finally more mind . . ." The trouble with this definition is that it lacks all rigour; it is useless in any exact or quantitative work. Those guilty of "geneticism" wish to measure natural selection instead of merely talking about it. This is not to deny that there has been improvement, functional efficiency, organization, adaptation, self-regulation, and mind in evolution, and that natural selection has been instrumental in producing all these good things. I shall, nevertheless, persist in my "geneticism," and maintain that natural selection does not always or necessarily yield these things. The concepts of natural selection and of fitness have evolved and changed since Darwin and Spencer; so have other fruitful concepts in science. Our concept of species is not identical with that of Linnaeus, and of gene with that of Mendel, Johannsen or Bateson. Owners of Greek dictionaries may, of course, manufacture new and fresh terms. I do not find this either expedient or attractive.

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SIR JULIAN HUXLEY writes: What I disagree with in Professor Dobzhansky's point of view, as set forth in his remarkable book, Mankind Evolving, are his statements that fitness, or as he prefers to call it, Darwinian fitness, is "measurable only in terms of reproductive proficiency", that "natural selection means differential reproduction of carriers of different genetic endowments", and that "the only trend or direction discernible in life and its evolution is the production of more life."

He now seeks to rebut my counter-statement that natural selection "generates what Darwin loosely called improvement, but which can be more precisely specified as an anagenetic trend towards higher grades or levels of organization permitting a more efficient utilization of the resources of the total environment", by the statement that this sort of definition lacks all rigour and is useless in any exact or quantitative work; and persists in equating his Darwinian fitness with selective value or adaptive value, and in asserting that "natural selection tends to maintain or enhance the Darwinian fitness." On this, I fear that I must continue to disagree with him. Of course, we can express Dobzhansky's Darwinian fitness in beautifully exact and quantitative terms. However, when we have done so, we have not measured the result of natural selection. but only the strength of one of the mechanisms through which natural selection operates.

I expect that our disagreement will turn out to be largely semantic. Conflicting points of view can often be reconciled by a restatement of the problem at issue. In my lifetime the conflict between the biometricians and Mendelians has been reconciled by being restated in terms of particulate inheritance and the selection of variants of small extent, and that between the environmentalists and their opponents in terms of modern epigenetic theory and genetic assimilation. I am confident that my conflict of views with Professor Dobzhansky and the population geneticists will be reconciled by a restatement of the real problem at issue, which is that of evolutionary improvement through natural selection.

As I suggested in my review of his book, there are really two distinct forms of natural selection —survival selection operating by the differential survival of phenotypes to maturity, and reproductive selection, operating by their differential

<sup>\*</sup> Eugen. Rev., 1962, 54, 123-141; Persp. Biol. Med., 1962, 5, 144-148.

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reproduction. Darwin's sexual selection through female choice is a form of reproductive selection, and provides a good example of the difference in the effects of the two selective processes; very high differential reproductive advantage may produce results disadvantageous to phenotypic survival, as in the males of polygamous birds like Argus Pheasants. In general, reproductive selection in my sense may often produce intra-specific results which are opposed to those resulting from inter-specific competition and are deleterious for the species as a whole. In many cases, however, the two processes go hand in hand, since many mutations simultaneously promote both phenotypic survival and reproductive success. Yet in

general they are distinct; reproductive selection may readily favour short-term ends which, in the long run, are injurious for the continued evolutionary improvement of the species or type, notably in difficult conditions. This is precisely what it is doing now in industrially advanced human societies.

If we accept that evolutionary improvement involves increased potentiality of long-term survival and multiplication of a strain, species or type, we have a criterion for evaluating the shares of phenotypic and reproductive selection in the evolutionary process, and the conflict of views over what constitutes fitness, Darwinian or otherwise, will be by-passed.

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